

A TAPHONOMIC AND DIAGENETIC CASE STUDY OF A PARTIALLY ARTICULATED ICHTHYOSAUR

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ABSTRACT. A single carcass of the large Middle Jurassic ichthyosaurian *Ophthalmosaurus* sp. was rapidly decomposed in well-oxygenated bottom water of the Lower Oxford Clay Midlands basin. Parts of the soft tissues lying within anoxic sediments were subjected to slower rates of decay and portions of the integument are now preserved as replacements by bacterial and possibly fungal mats. Elements of the skeleton were encrusted with epibionts on their upper surfaces. Burial diagenesis has significantly affected some skeleton elements, with the infilling of voids with calcite, pyrite, and sphalerite. Rarely, bone phosphate has been replaced by pyrite. Compaction of bones and septarian cracking of surrounding concretionary mudstone has caused crushing and brecciation of trabecular bones. More massive bones with cross-sections capable of transmitting overburden pressures have resisted compaction.

THE partial skeletal remains of an ichthyosaur, *Ophthalmosaurus* sp. were discovered (by Mr Lez Fitchett, an employee of French Kier Construction) in the autumn of 1982 at Milton Keynes, Buckinghamshire, during the construction of Caldecotte Lake. The specimen has been examined in detail whilst still *in situ* and has formed the basis of a case-study on the preservation of marine vertebrates in bituminous shales. The skeleton is now a mounted specimen in Milton Keynes Public Library, BCM 1983/1008.

A systematic excavation of the specimen was undertaken between 12 October 1982 and 15 October 1982. Samples of the surrounding sediment were collected with the specimen for micro-palaeontological and sedimentological analysis.

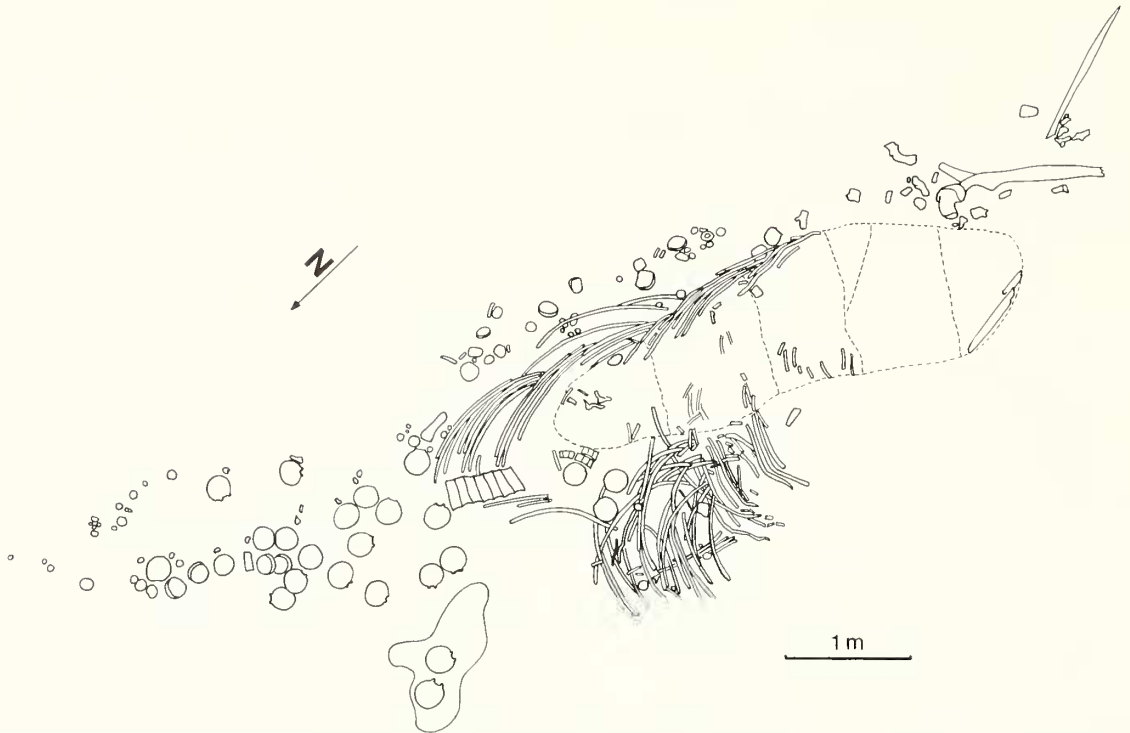
The specimen is that of a mature adult, approximately 5 m long (text-fig. 1). Some skeletal elements do not appear on the diagram as they were disturbed by the excavating machinery, and cannot be accurately positioned. Misplaced elements include part of the coracoid, the right? ulna, part of the rostrum, and numerous digits. Part of the right side of the rib cage was also slightly disturbed.

Horizon. The stratigraphic distribution and preservation of fossil vertebrates in the Lower Oxford Clay has been discussed by Martill (1985, 1986). The skeleton was found in the Lower Oxford Clay (Middle Callovian, Middle Jurassic), lying partly within greenish bituminous shale and enclosed by a large septarian concretion. Two thoracic vertebrae detached from the main part of the skeleton were enclosed in a pyrite concretion. There is no published lithological section for the site, but a section for the nearby brick pits at Bletchley is given by Callomon (1968) and probably differs only in minor details.

Beds 17 and 9 of Callomon's section can be identified in the site at Milton Keynes, and from a comparison of the concretion with those occurring at Bletchley it appears that this specimen is from bed 9. Thus the skeleton is from the obductum Subzone of the coronatum Zone.

Locality. Caldecotte Lake is situated on the South side of Milton Keynes at National Grid Reference SP 892 352. Excavation of the site is now complete and all exposures of the Oxford Clay have disappeared due to flooding and landscaping of the site.

Taxonomy. The skeleton is that of an associated, partially articulated *Ophthalmosaurus* sp. Specific identification cannot be determined as the diagnostic coracoids (Appleby 1956) are not sufficiently well preserved to show the anterior and posterior notches. Two species of *Ophthalmosaurus* are



TEXT-FIG. 1. Outline skeletal plan of *Ophthalmosaurus* sp. BCM 1983/1008 as found *in situ* at Caldecotte Lake, Milton Keynes, Buckinghamshire. Certain elements of the skull and shoulder girdle are omitted from the plan as they were disturbed by earth-moving machinery.

recorded from the Lower Oxford Clay; *O. icenicus* Seeley 1874, and *O. monocharactus* Appleby 1956. The differences between the two are small, and considering the degree of variability seen within *Ophthalmosaurus*, the differences may be sexual (Andrews 1910).

MATERIAL AND METHODS

The specimen consists of a partially articulated skeleton wanting only a few elements. Due to intense brecciation it is not clear which elements are present in the concretion. Those parts of the skeleton known to be preserved include all of the posterior portion of the vertebral column from about the ?20th vertebrae to the tip of the tail. A few of the neural arches, especially the more posterior ones are present. Of the skull there is a right quadrate, left and right lachrymals, right coronoid, right dentary, angular and surangular, and portions of the left and right premaxillae. There are also a few plates from the sclerotic ring. The rib cage is almost complete, although the right side is very disarticulated. The fore limbs are represented by left and right radii, left and right ulna, and numerous carpals and metacarpals. A highly brecciated humerus was found within the concretion. The left ischio-pubis, left femur, and fused left tibia and fibula were found with numerous digits.

The skeleton was found lying in clay, grey/green, rather tenacious and slightly bituminous, and was partly enclosed by a large septarian concretion. Two detached vertebrae were found enclosed in a flat pyrite concretion. The following excavation procedure was carried out so that the skeleton could be removed to the laboratories of the Geology Department of the University of Leicester for cleaning, preparing, and subsequent mounting.

1. The skeleton was completely exposed *in situ* by careful digging with knives, forks, spoons, and small trowels. Where the overburden exceeded more than a few centimetres a spade was employed.

2. The exposed skeleton was overlain with clear acetate sheeting and the position of all the bones was mapped out using an indelible ink marker pen. Each bone received a unique number on the plan and was placed in a scalable polythene bag bearing the same number. Where the bone was broken into two or more pieces, all of the pieces were placed in the same bag.

3. Fractured elongate bones of the lower jaws were collected in their entirety by excavating around them until they were left lying on an elevated plinth of clay. The clay plinth was undercut using a 'cheese wire' technique and a length of square section guttering slid underneath. This was then lifted and individually wrapped to protect the fragile bones during transit.

4. The specimen was removed to the laboratory for cleaning. During this stage a black and buff coloured surface coating was discovered on the surfaces of some of the bones. Cleaning of the bones was achieved by soaking in warm water using only mild detergents to assist break down of the clay.

5. Removal of hard rock (mainly fibrous calcite) adhering to bones found in the clay was achieved by use of a pneumatic chisel (*Vibrotool*) and steel needles.

6. Bones in the concretion were considered unsuitable for use in the reconstruction of the skeleton, but were used for diagenetic studies. The large calcareous concretion was cut up with a rock saw. Thin sections were made from the remaining fragments. Bone used for scanning electron microscopy was extracted from the matrix using 10% acetic acid.

7. Prepared bone was examined by light and scanning electron microscopy. Bone coatings were examined by both scanning and transmission electron microscopy. Mineral phases were identified using normal petrographic thin sections.

TAPHONOMY

The remains constitute an associated skeleton of a single individual. Much of the skeleton is disarticulated, but a few elements, notably the left side of the thoracic ribs are articulated, and show true bone to bone relationships, as in the living animal. Some skull elements enclosed within the concretion, and the anterior part of the rostrum disturbed by the excavator, are also articulated. The remainder of the skeleton is disarticulated, but most of the individual bones have not been moved from their original positions by more than a few centimetres. Thus the overall shape of an ichthyosaur skeleton is retained.

The cause of death of the animal cannot be satisfactorily determined. Advanced ossification, indicated by irregular expansions to the ends of the ribs, and by fusing of the left tibia and fibula suggest it was an old animal. There is little disruption of the skeleton to suggest the animal was the prey of a large carnivore such as a pliosaur, so it is likely that it died of old age or disease.

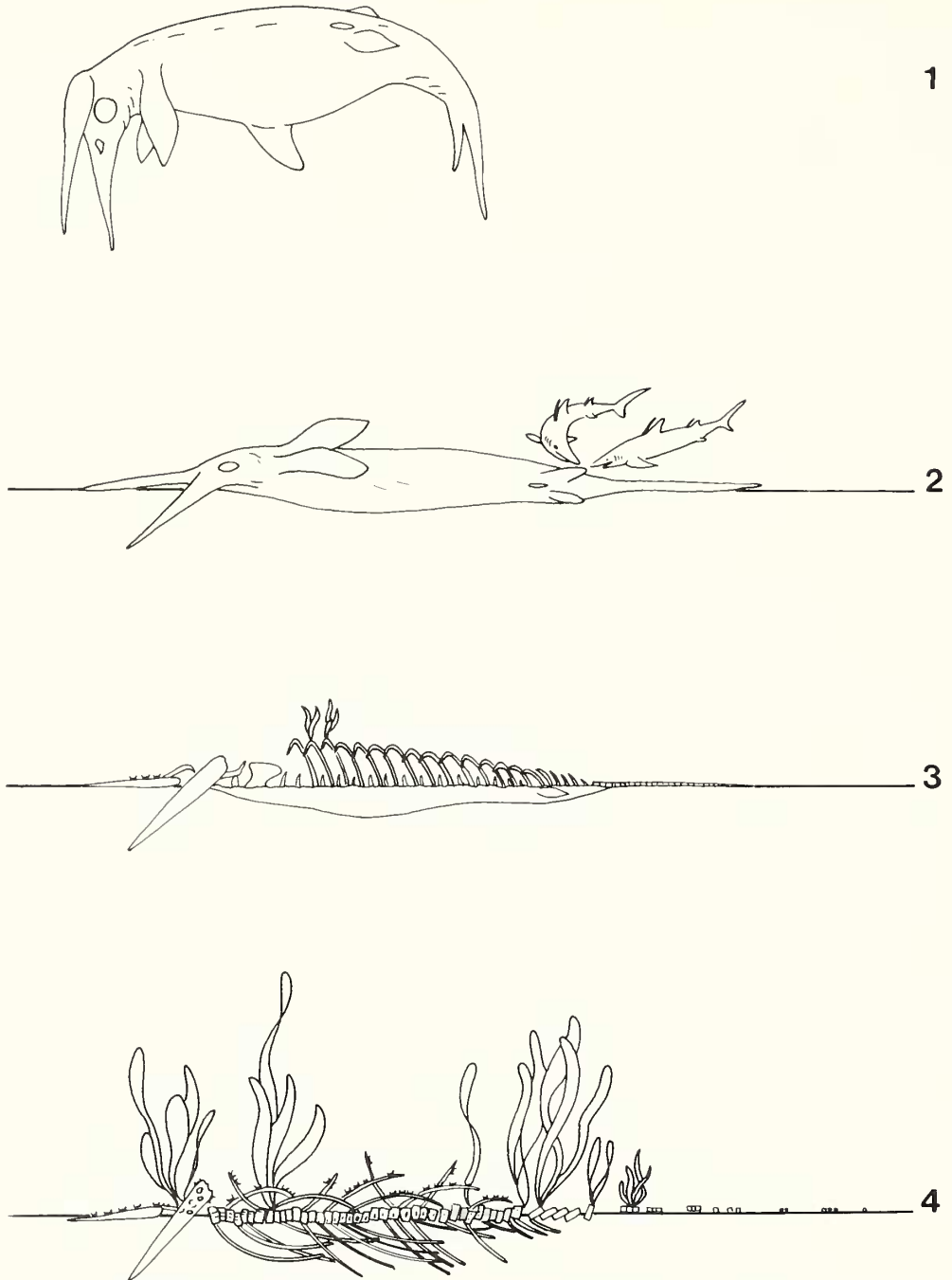
Apart from the right hind limb, all appendages are present, including the extreme tip of the tail. This indicates that very little scavenging took place during post-mortem drifting, with only the right rear paddle possibly missing due to scavenger activity. The carcass arrived on the sea-floor intact, with most of the soft tissue present, serving to hold the skeleton together.

The position of the skeleton, lying on its left side suggests that it landed on the sea-floor ventrally, and as the flesh decomposed the skeleton collapsed forwards and on to its left side.

The carcass descended to the sea-floor with a velocity sufficient to allow the tip of the rostrum to penetrate the sediment. Penetration of the rostrum tip into the sediment indicates that the skull arrived on the sea-floor first, and may have been suspended below the main body of the carcass. Presumably the sediment was soft, possibly even soupy, and the sinking velocity of the carcass need not have been great.

Decomposition of the soft tissue in the water column took place rapidly and left the right side of the rib cage exposed to sea water. Soft tissues in contact with the sediment decomposed more slowly, and in the case of some of the tissues which had sank into the sediment, decomposition was not completed. Text-fig. 2 summarizes the taphonomic history of the specimen.

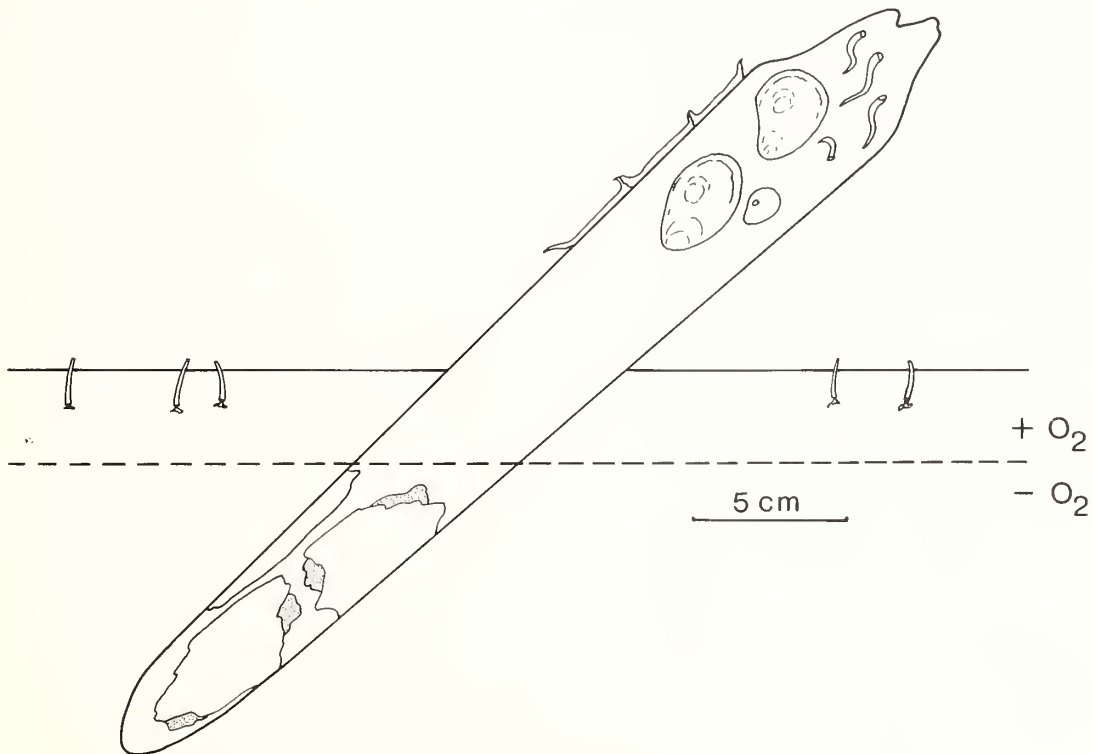
The bottom waters of the Lower Oxford Clay Midland basin were in general well oxygenated and capable of supporting a diverse benthos (Duff 1975). The clays around the specimen, however,



TEXT-FIG. 2. Summary of taphonomic history of BCM 1983/1008 based on observations made from position of skeleton and state of preservation of skeletal elements. 1, carcass drifts in water column with skull suspended below main body of carcass. 2, carcass descends to sea-floor and part of rostrum penetrates sediment. Light scavenging may take place. 3, rapid decomposition of soft tissues in well oxygenated bottom water. 4, collapse of skeleton and encrustation by epibionts.

yielded only a restricted benthos of nuculacean bivalves, scaphopods, and foraminifera; although the latter cannot be definitely considered benthic. Oysters and serpulid worms were found encrusting the skeleton but were not found in the surrounding sediment (see below). This suggests that the skeleton acted as a benthic island. Sea water in contact with the sediment may have been slightly depleted in oxygen, and the oysters and serpulids encrusting the skeleton survived due to their elevated position in more oxygenated water. If this is the case then current activity must have been at a minimum to prevent mixing of the oxygen-depleted water with the oxygen-rich water. However, this is not the only mechanism for producing the restricted infauna; the soft substrate may also have been a contributing factor. The restriction of the benthos limited scavenging of the carcass while on the sea-floor, but the movement of a few bones, notably the two vertebrae in the pyrite concretion, is not due to current activity, and can almost certainly be attributed to scavenging. Current activity is ruled out on the grounds that the two vertebrae are large and a current strong enough to move them would have also moved the smaller elements of the skeleton. If seaweed grew on the surface of the bones, it is possible that added buoyancy might assist movement during storm activity. It is, however, difficult to establish if the skeleton lay within the photic zone.

Epibionts. Many of the disarticulated elements of the skeleton are pale buff in colour. These bones are frequently encrusted with epibionts, including oysters and serpulid worms. The oysters are only found encrusting the buff coloured bones, and are restricted to the upper surfaces (text-fig. 3). No micro-epibionts have been found on the underside of the skeleton, or on the dark brown bones of the articulated portions of the skeleton. The oysters are preserved in dark grey calcite. They frequently reach a length of 4 cm, and on flat bones they remain attached continuously during



TEXT-FIG. 3. Portion of rostrum having penetrated soft sediment. Soft tissues are preserved below oxygen minimum zone. Epibionts encrust bone in well oxygenated water.

ontogeny. Oysters encrusting bones with strongly curving surfaces, i.e. ribs, are only attached during early ontogeny, later stages of shell growth migrate away from the bone surface and the oyster shell becomes curved. On very smooth bone surfaces the oyster may not secrete shell material, but lie in direct contact with the bone.

Serpulid worms are less common than oysters, and are usually small, being generally less than 1 cm long. They are preserved as white calcareous conical tubes, approximately 2–3 mm diameter anteriorly. No geotropism or phototropism has been established, but the distribution pattern on the skeleton follows that of the oysters.

Soft tissues. The undersides of the articulated parts of the skeleton are dark brown, and devoid of epibionts. A black coating adheres to the underside of the articulated vertebrae that lie within the shale, and also to the underside of some of the ribs from the left side of the rib cage. (In life this would be the outer surface of the left side of the rib cage.) The black coating, overlain by a slightly reflective white/buff coating was also found on a portion of the premaxilla.

These coatings are restricted to the dark brown coloured bones. No oyster encrustations are found on the dark brown bones which suggests that these bones were in contact with, and partly buried in the sediment. The black and white coatings may be by-products of a decomposing integument (Pl. 63, figs. 1 and 2). The abundance of pyrite within the sediment and encrusting some of the bones shows that reducing conditions were present within the sediment. If the oxic/anoxic boundary was close to the sediment water interface, the penetration of the ichthyosaur carcass into the sediment may have introduced some of the soft tissues to reducing conditions, thus reducing the rate of decay.

Scanning electron microscopy of the black coating from the underside of the vertebral column shows it to be composed of an amorphous mass of carbonaceous material, underneath which are numerous ovoids approximately 1 μm long, and about 0.5 μm diameter (Pl. 63, figs. 3 and 4). These ovoids are interpreted as lithified bacteria, similar to those reported from soft-part outlines of Eocene frogs and bats (Wuttke 1983). The bacteria represent a replacement of some of the original soft tissues. In the case of the ichthyosaur *Stenopterygius* spp. from the Posidonia Shale (Toarcian, Lower Jurassic) of Holzmaden, West Germany, these black coatings may extend into the sediment to produce an outline of the entire animal (McGowan 1979). In the Lower Oxford Clay the micro-environment in which this process can occur was restricted to the undersides of bones lying within anoxic sediment, and has prevented complete outlines from being preserved.

DIAGENESIS

Apart from compaction and mineralization effects the skeletal elements are preserved in two distinct ways: as dark brown bones with a smooth surface; or, as light buff bones with a soft powdery surface. The powdery surface is considered to be an effect of prolonged exposure to sea water, but might also be attributable to the encrusting of the bone surface by marine algae. Internally, the light buff bones are indistinguishable from the dark brown bones. Parts of the rib cage of the right side of the skeleton were freshly fractured due to the weight of the earth-moving machinery. It can be seen that in some of the ribs no mineralization of the voids in the bone has taken place. This has

EXPLANATION OF PLATE 63

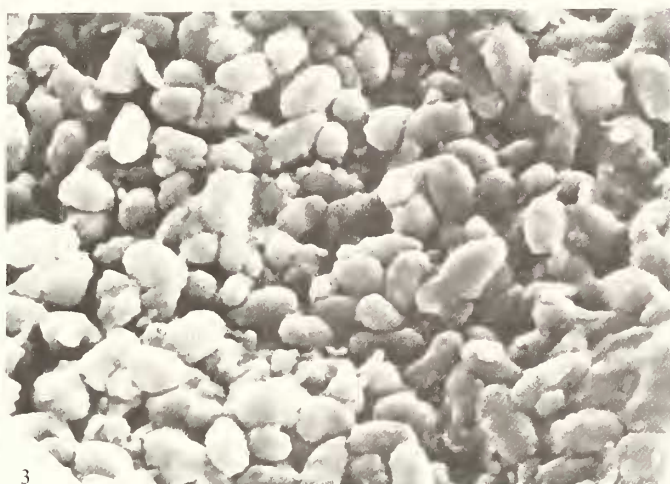
Preserved bacterial mats on surface of ichthyosaur bones.

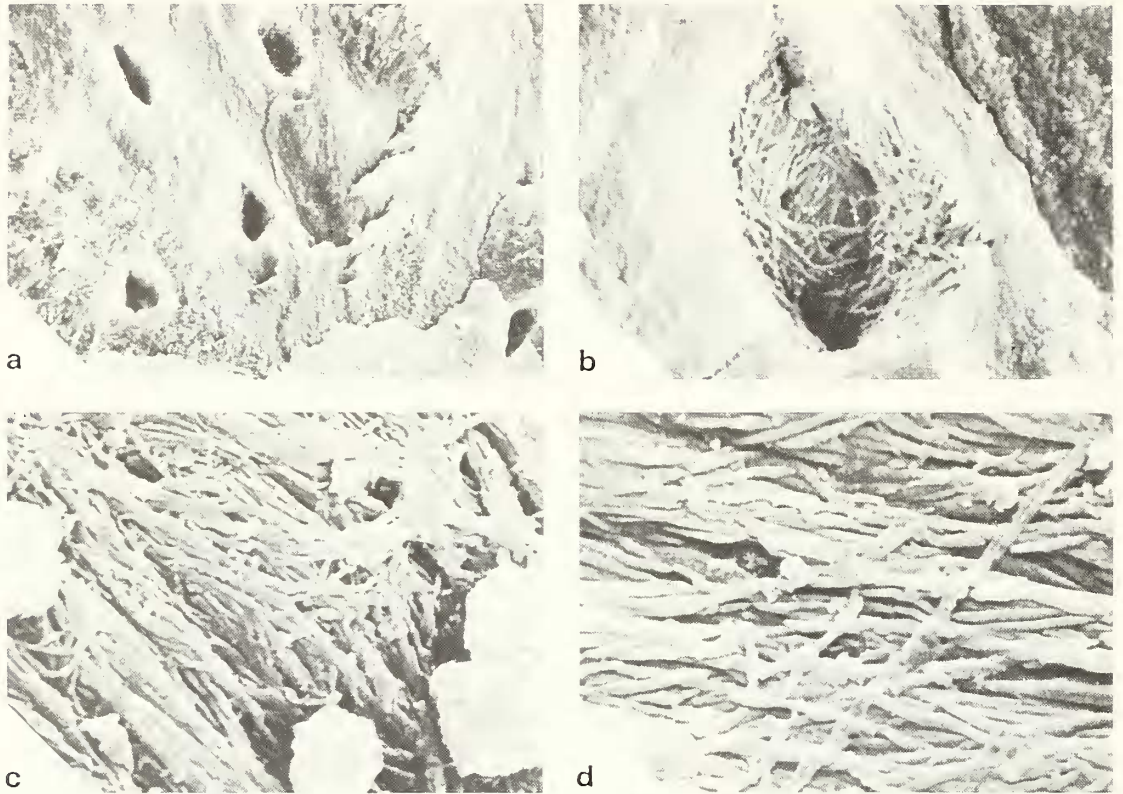
Fig. 1. Rostrum of *Ophthalmosaurus* sp. BCM 1983/1008, showing black film overlain by buff coloured reflective coating. $\times 1$.

Fig. 2. Underside of thoracic centrum of *Ophthalmosaurus* sp. BCM 1983/1008 showing black film only. $\times 1$.

Fig. 3. SEM of lithified bacteria composing black film. $\times 10\ 000$.

Fig. 4. Transmission electron micrograph of ultra thin section from black film taken from below thoracic vertebrae showing electron dense bacterial bodies. Osmium stained. $\times 30\ 000$.





TEXT-FIG. 4. Ultra structure of bone from *Ophthalmosaurus* sp. revealed by SEM after preparation in 10% acetic acid. *a*, portion of jaw showing lacunae. $\times 100$. *b*, detail of single lacuna with lining of newly mineralized collagen fibrils. $\times 400$. *c*, tangled webs of mineralized collagen fibrils from vertebral centrum overgrown by small euhedral pyrite crystallites. $\times 520$. *d*, bundles of collagen fibrils twisted in rope-like fashion from highly trabecular vertebral centrum. $\times 900$.

made the bones very fragile. In other bones, however, the void spaces have been filled with a variety of mineral phases (see below), and are more robust. Scanning electron microscopy of both the bone surface and fractures of bone trabeculae etched in acetic acid show that no alteration of the phosphatic bone matrix has taken place during burial diagenesis.

Bone ultra-structure. Thin sections and acetic acid etched samples of the bone show that the phosphatic matrix of the bones from this specimen have remained relatively unaltered since the death of the animal, and that the structures observed in thin sections, and with the electron microscope, are primary features. In thin section the trabecular bone of vertebrae and ribs is seen to be rich in lacunae and canaliculae, most of which have remained as voids within the bone; only in a few sections have these been filled with diagenetic minerals, notably pyrite. High power scanning electron microscopy of the internal surface of lacunae (text-fig. 4*a, b*) shows an irregular mass of phosphatized collagen fibres, which at ultra high-power show evidence of banding. The surface of the bony trabeculae is likewise unaltered, even after the effects of mineralization. Parts of a vertebral centrum filled with late ferroan calcite were etched in 10% acetic acid until all the carbonate phase had been removed. An examination of the prepared surface showed bundles of phosphatized collagen fibrils lying roughly parallel to the surface of the trabeculae. These are occasionally transgressed by isolated fibrils of phosphatized collagen. In some parts of the bone the parallel

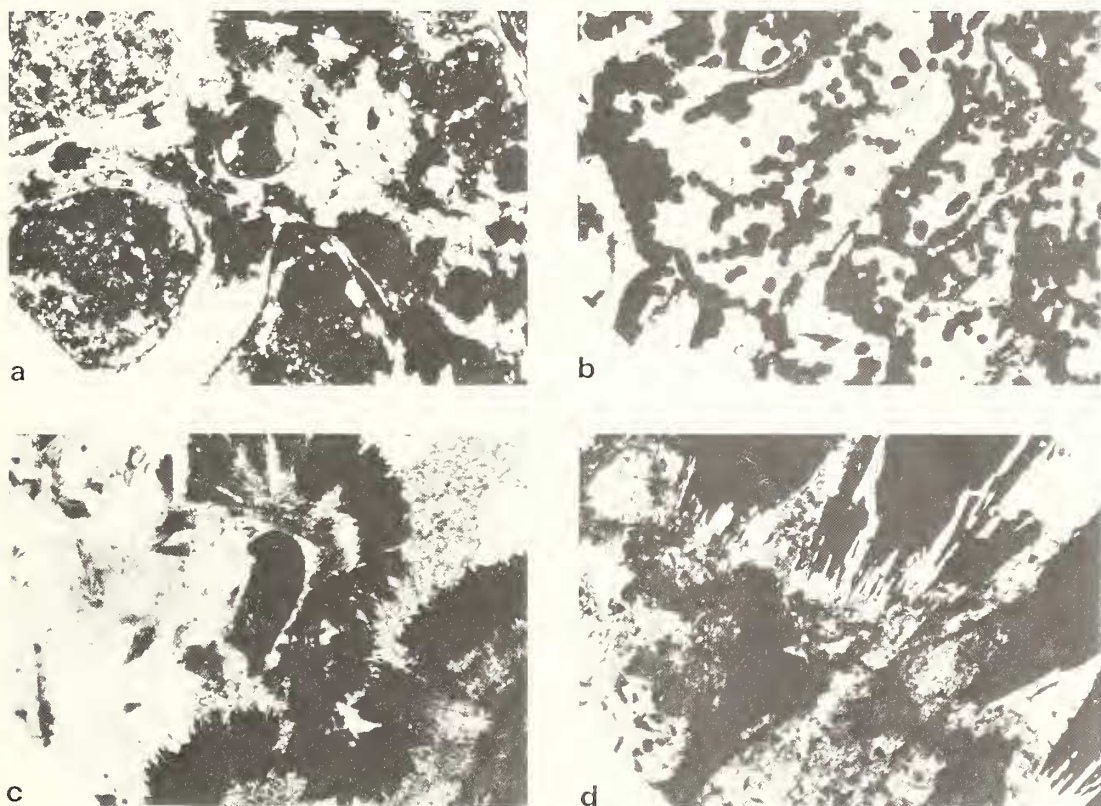
fibrils become tangled masses, and single bundles may bifurcate (text-fig. 4c, d). Each bundle of phosphatized collagen consists of nine or more individual fibrils, all of which are entwined like rope. The bundles are approximately $3\ \mu\text{m}$ diameter, with individual strands less than 200 nm diameter. The longest individual strands are over $9\ \mu\text{m}$ long, but the bundles are several times longer than this.

Good resolution work at high power is difficult to achieve, but when possible, the banding on the phosphatized collagen fibres appeared to be due to spaces 15 nm across, between individual crystallites of apatite approximately 100 nm across. The organic matrix of the bone was not present.

Diagenetic minerals

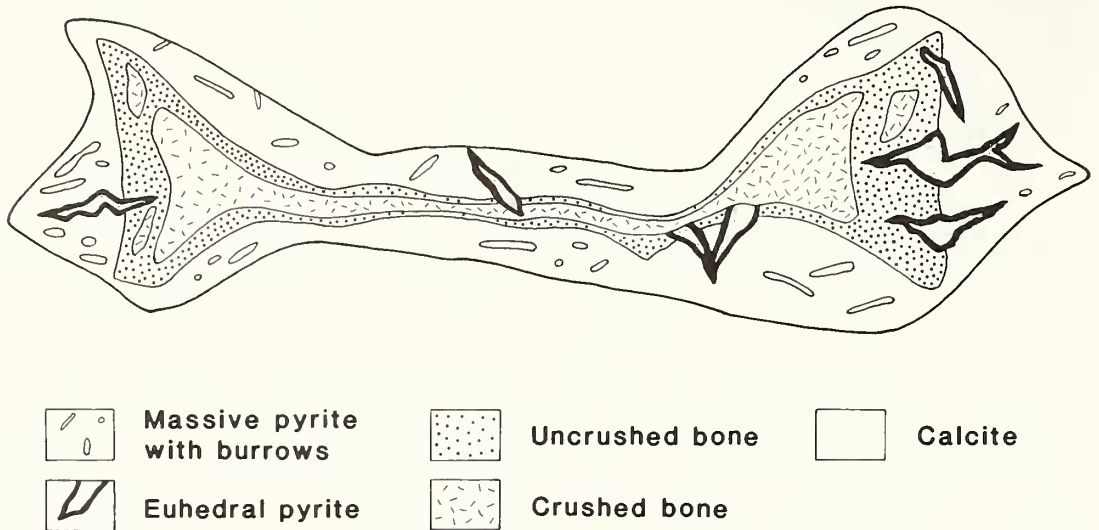
Pyrite. No alteration of the original mineral matrix of bone has taken place in those elements found within the shales or the large calcareous concretion, but there has been some replacement of phosphatic material in the two thoracic vertebral centra preserved in the pyrite concretion. Thin sections of the pyrite concretion show that lacunae and canaliculae, and void spaces in the trabecular parts of the bone are filled with pyrite. In some parts of the concretion the pyrite appears to have spread outwards from lacunae and pyrite filled voids to replace the bone material itself (text-fig. 5a).

Pyrite is also abundant in the trabecular bone as aggregates of pyrite octahedra. The aggregates



TEXT-FIG. 5. Thin section through over pyritized trabecular bone. *a*, pyrite (black) filling lacunae, void spaces, and partially replacing bone. $\times 20$. *b*, chains of pyrite framboids on surface of bone. $\times 20$. *c*, blade-like pyrite possibly pseudomorphing marcasite growing tangential to bone surface. $\times 20$. *d*, detail of blade-like pyrite. $\times 20$.

may completely fill voids in the bone, but frequently aggregates are less than $1\ \mu\text{m}$ diameter and pyrite crystallites may represent the activity of a single sulphate reducing bacterium. These aggregates are seen in thin section as rounded bodies, isolated or in chains (text-fig. 5*b*). Individual octahedra are less than $3\ \mu\text{m}$ diameter, but are well-formed crystallites, whereas the aggregates are up to $20\ \mu\text{m}$ diameter, but the crystallites are less distinct, giving the aggregates a granular appearance.



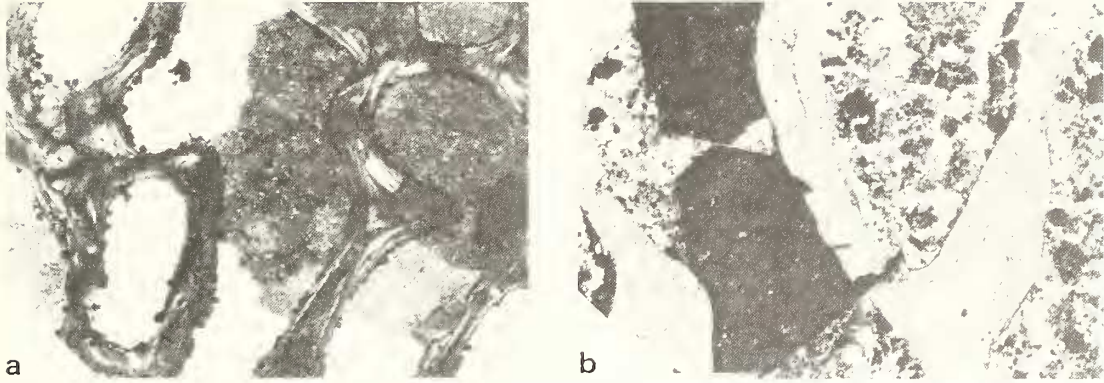
TEXT-FIG. 6. Disc-shaped pyrite concretion overgrowing thoracic centrum. Pyrite formation has preserved burrows in the sediment and prevented the centrum from suffering severe compaction damage, but some crushing has still taken place. Septarian cracking of the concretion has also affected the bone.

Concretionary pyrite is abundant in parts of the Lower Oxford Clay where it can be found overgrowing ammonites and fossil wood. It commonly forms flat disc-like concretions in the plane of the bedding. The concretionary pyrite on the two vertebral centra of this specimen is of a similar habit (text-fig. 6). Each vertebra is totally overgrown, and extensions of the pyrite extend horizontally, uniting the two centra. Two forms of pyrite are present, an amorphous pyrite mudstone found on the outside of the centra, and a micro-crystalline pyrite found lining void spaces in the bone, and lining later fractures in the amorphous pyrite.

The bone within the pyrite concretion has a few microfractures, and has been subjected to slight compaction, but it is apparent that the bones in the pyrite concretion have resisted compaction more than the bones in the shales.

Sphalerite. Small quantities of euhedral sphalerite are found in early fractures between bones, in large voids in trabecular bone, and in the tooth groove of the premaxilla and dentary. Occasionally sphalerite is found on the surface of the bone, but it appears to be most common in areas that have not been subjected to compaction. Sphalerite post dates in part the main compaction phase, as it can be found filling cracks in brecciated bone and surrounding bone shards (text-fig. 7*b*), but it is not found in fractures in the large calcareous concretion. It is considered to be of a later origin than the pyrite, post compaction of the bone, but pre-brecciation of the concretion.

Calcite. Late ferroan calcite is abundant, and found filling voids in bones, small fractures in the pyrite concretion, and large fractures in the calcareous concretion. In uncompacted trabecular bones it is found as coarse crystals completely filling cavities (text-fig. 7*a*). Crystal boundaries are irregular, suggesting some pressure solution at the boundaries. No fringing cements have been observed.



TEXT-FIG. 7. Void filling minerals in trabecular bone. *a*, trabecular bone with coarse-grained ferroan calcite filling void spaces. Crossed nicols. $\times 20$. *b*, euhedral sphalerite (dark grey) filling void and fracture in trabecular bone (light grey) with later ferroan calcite (mottled). Transmitted light. $\times 20$.

Many of the bones in the bituminous mudstone are coated with fibrous ferroan calcite (beef) up to 2 mm thick, with a thin film of clay sandwiched in between. This fibrous coating causes problems for the preparator as it requires removal with a vibrotool.

COMPACTION

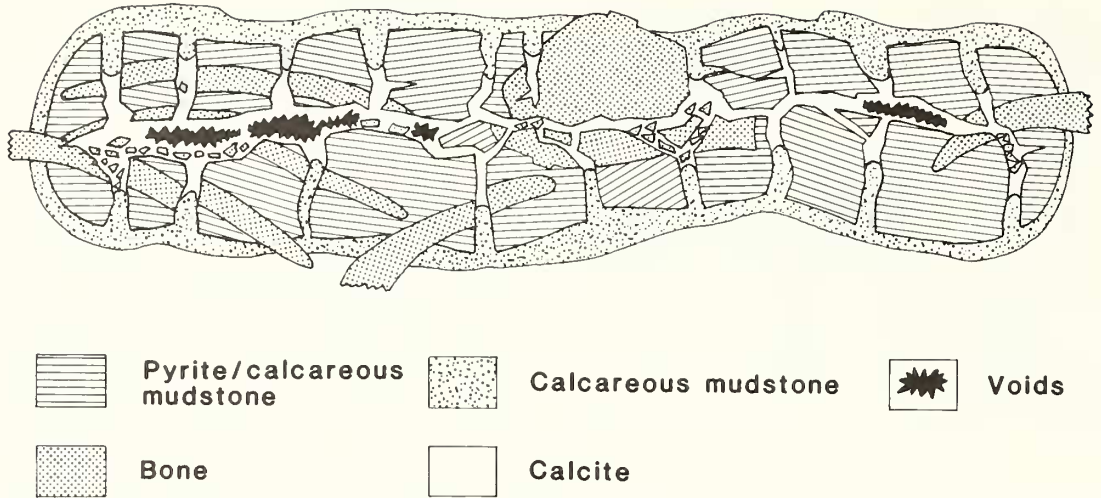
Compaction has had a deleterious affect on the specimen, and has resulted in differential preservation of the skeleton. Many of the elements of the skeleton that were lying within the bituminous mudstone have been uniaxially flattened by compaction. Failure of the bones is of a brittle nature, often with the complete shattering of all the inner trabeculae. The more solid margins of bones have resisted compaction, as have those bones with shapes that can transmit overburden pressures around their surface.

Compaction of some of the vertebrae has been greater than 50 % and has been unaffected by the position of the bone in the sediment. Vertebrae lying flat on the bedding planes have been flattened anteroposteriorly, while those lying vertically are flattened dorsoventrally. Confining pressure of the sediment has kept the brecciated bone together, and later cementation by ferroan calcite has allowed individual bones to be collected entire, although severely crushed. During acetic acid preparation the compacted elements of the skeleton fall into thousands of bone shards most of which are less than 1 mm long.

Early formation of the calcareous concretion has prevented bones enclosed by the concretion from being compacted, but compaction has caused the concretion to brecciate (Hudson 1978). Wide cracks have developed in the concretion which have penetrated the bones. Geopetal fabrics can be observed where shards of bone have fallen to the bottom of the cracks (text-fig. 8). Uncompacted clay has been squeezed into the cracks, and has penetrated cavities in the bone. Differential movement of the brecciated concretion and re-cementation of the fragments by coarsely crystalline ferroan calcite has resulted in a bone breccia.

Formation of the pyrite concretion appears to have post-dated the formation of the calcareous concretion, as the two vertebral centra preserved within the concretion show a slight degree of compaction, but this is not as severe as that which affected the bones in the shale.

Compaction has not affected the microstructure of the most highly compacted vertebrae, where lacunae and canaliculae can still be observed. Thus failure due to compaction is entirely of a brittle nature, with no observable alteration due to pressure solution or recrystallization. All fractures are clean and sharp and some appear to be controlled by the cleavage of void filling calcites.



TEXT-FIG. 8. A composite section through mudstone concretion illustrating diagenetic and compactional features affecting the preservation of enclosed skeletal elements of *Ophthalmosaurus* sp. Part of BCM 1983/1008.

CONCLUSION

The Milton Keynes specimen of *Ophthalmosaurus* died as a large adult, with disease possibly being a contributing factor to its death. The carcass sank rapidly to the sea-floor and was almost unaffected by scavengers. It lay partly buried in the sediment, where parts of the soft tissue underwent a long slow period of incomplete degradation by sulphate-reducing bacteria. The upper part of the carcass underwent rapid decomposition, and the exposed skeleton was encrusted by a restricted, but abundant epifauna. Parts of the skeleton became detached due to a combination of benthic scavenging, drifting due to adhering seaweed and perhaps storm activity. After burial, early formation of a calcareous concretion occurred around the anterior part of the post cranial skeleton. Compaction due to burial crushed many of the more trabecular, and flat bones, and also caused brecciation of the concretion, but later compaction caused some septarian cracking of the pyrite concretion also. Small quantities of sphalerite formed in lower pressure areas after an initial compaction phase. The three broad preservational styles in which this specimen occurs; in compacted shale, calcareous concretion, and pyrite concretion, are typical of vertebrates in the Lower Oxford Clay of the South Midlands, but at Peterborough pyrite is less abundant and normally only found as thin films on the surface of bones. At Peterborough septarian concretions occur around vertebrates in the Jason Zone (Martill 1985), although septarian, brecciation is generally less severe than in concretions from the Milton Keynes district.

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